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Tamm Review: Insights gained from light use and leaf growth efficiency indices

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A B S T R A C T

In this Tamm review, we trace the origin and application of two production indices: Light Use Efficiency (*LUE*) and (Leaf) Growth Efficiency (*GE*). Light Use Efficiency usually denoted (ε) was originally defined by John Monteith in the 1970s as the rate that dry matter is accumulated by plants in relation to the amount of solar radiation absorbed by leaves; the concept has been a corner-stone of the field of production ecology ever since. Although highly variable at daily intervals, *LUE* becomes linear at longer intervals, providing a major simplification to the construction and application of process-based models. A further simplification in model construction became possible when it was found that the ratio between total dry mass production and gross photosynthesis is approximately constant (≈0.5). Simplified process-based models provide a means of estimating the maximum productivity of a species growing inside or outside its native range, and help to identify constraints on production in current and projected environments. Consequently, models that incorporate *LUE* have expanded from research tools to practical ways of assessing silvicultural options in the management of individual forests as well as for measuring and forecasting global trends in forest productivity. The Leaf Growth Efficiency (*GE*) index, defined as annual growth in stemwood per unit of leaf area, has become widely adopted as a means of identifying the spatial variation among trees, which affects stand growth and *LUE*. *GE* was originally used to assess the vulnerability of individual trees to attack by bark beetles but, combined with structural and physiological analyses it has been found useful for interpreting and predicting stand growth responses to tree spacing, aging, and defoliation. Challenges remaining in the field of forest production ecology include prediction of the effects of fast-changing climatic conditions across the globe on the growth and survival of species, and their interactions with continually rising atmospheric concentrations of CO_2.

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1. Introduction

In 2013 Forest Ecology and Management launched a review series designed to highlight the most important issues that affect the future of forest ecology and management around the world. The series is named in honor of the Swedish forest ecologist, Carl Olof Tamm who, in a career spanning more than 50 active years, made important contributions to forest ecology, forest production ecology and soil science. Most of his research and teaching were done in Sweden, but he made important contributions to international discussions and the development of environmental policies in Europe during the 1980s and 1990s. Tamm's career and contributions to forest science were summarized in an earlier Tamm review by Högberg and Linder (2014). In the present review we offer a summary and assessment of two concepts that have contributed significantly to the development of a quantitative approach to the field of forest production ecology: light use efficiency (*LUE*) and leaf growth efficiency (*GE*).

Over the last forty years, production ecology has progressed (and matured) from simply quantifying standing biomass (carbon stores) to predicting current and future growth rates in response to changing environmental conditions. The development of the two indices—Light Use Efficiency (ε) and Growth Efficiency (*GE*) — has been critical in helping the field to advance. Both indices originate in agriculture but their application to forests, which often grow in more stressful environments than cultivated crops, has provided the scientific underpinnings of most process-based growth models and the basis for sound management practices designed to improve and maintain healthy forests.

In this review, we trace the origins of the two indices and identify the steps in their development and application that have led to quantitative predictions of yields under changing climatic conditions, as well as identifying thresholds that indicate the vulnerability of individual trees to attack from native insects and pathogens. Not surprisingly, there are many cross-linkages between the two, as insights gained from one often offer an explanation for responses observed with the other.

2. Light Use Efficiency (*LUE*)

2.1. Definition

Light Use Efficiency (*LUE*) provides a measure of the productivity of terrestrial vegetation in relation to the photosynthetically active radiation (PAR) absorbed by the leaves (APAR). PAR, representing visible light, constitutes about half the energy in the short-wave solar radiation incident on the earth's surface. *LUE* therefore measures the efficiency with which plant canopies convert the sun's energy into the chemical energy stored in the products of photosynthesis, mainly carbohydrates, measured as dry matter. Efficiency is, technically, dimensionless. Conforming to that convention, we would express *LUE* as the ratio of chemical energy produced per unit of solar energy absorbed (Q_{abs}), but in plant production ecology it is usually expressed in units of dry mass (DM) produced per unit of PAR absorbed.

2.2. Background

The connection between light and photosynthesis has been understood, at least in principle, since the early part of the 20th century, and it was obvious that there must be quantitative relationships between incident light and plant productivity. The first breakthrough in application of the Light Use Efficiency concept was provided by Monteith (1977), who demonstrated that dry matter accumulation by crops is linearly related to the amount of radiation intercepted by the plant canopy. The linear relationship provides a simple, robust model with only one parameter – the slope of the line, generally denoted ε. Epsilon is, in effect, a measure of the Light Utilization Efficiency of the plant community.

Monteith estimated the average value of *LUE* in terms of intercepted solar radiation and above-ground production of dry mass as 1.4 g DM MJ^{-1}, i.e. about 2.8 g DM MJ^{-1} absorbed PAR (APAR). The slopes of the lines for the four crops he considered — sugar beet, potatoes, barley and apples — were similar and linear but not identical. That *LUE* might be nearly constant and linear spurred activity to test the concept. Our aim here is to assess the general usefulness of the concept, the extent of, and reason for, variation in *LUE* and its application to production ecology at small and global scales. More comprehensive reviews of light use efficiency in natural and planted forests are presented by Landsberg et al. (1997), and for crops by Sinclair and Muchow (1999).

Jarvis and Leverenz (1983) were the first to make a thorough analysis and assessment of the application of the ε model to forests. They arrived at estimates of *LUE* for above-ground growth (ε_a) in relation to total solar radiation ranging from 0.15 g DM MJ^{-1} for warm area deciduous forests to 0.78 g DM MJ^{-1} for cool-area evergreens. (Those values would be doubled if the analyses were made in terms of PAR). The first convincing empirical demonstration that there might be a linear relationship between forest growth and intercepted light was provided by Linder (1985), who derived values of *LUE* of about 1.7 g DM MJ^{-1} (APAR) for above-ground (ε_a) production by plantations of *Eucalyptus* and Monterey pine (*Pinus radiata*). Since that time estimates of ε for total NPP and above-ground production have been obtained from a number of studies for a range of tree species.

Empirical values of ε_a have usually been calculated from biomass data obtained by destructive sampling, or careful measurements of tree growth, or some combination of these techniques. In most cases APAR was, and continues to be, estimated using Beer's Law with time-integrated values of PAR and consideration of seasonal changes in projected Leaf Area Index (*L*). The values for ε_a cited by Landsberg and Sands (2011; Table 5.1) ranged from 0.2 g DM MJ^{-1} to 2.73 g DM MJ^{-1} APAR. Most of the high values were obtained for wet, tropical eucalypts plantations while the lowest were associated with forests growing in much harsher environments. In the sections below we assess a range of possibilities that might explain the wide variation of ε_a.

2.3. Integration of absorbed photosynthetically active radiation

Good estimates of *LUE* depend on accurate estimates of the amount of light (photosynthetically active radiation) absorbed by

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